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DISCOVERY REPORTS

Vol. XXXI, pp. 299–326

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THE APPENDAGES OF THE HALOCYPRIDIDAE

by

E. J. Iles
(Department of Zoology, The University of Manchester)

CAMBRIDGE
AT THE UNIVERSITY PRESS
1961

Price 15s. net

PUBLISHED BY
THE SYNDICS OF THE CAMBRIDGE UNIVERSITY PRESS
Bentley House, 200 Euston Road, London, N.W. 1
American Branch: 32 East 57th Street, New York 22, N.Y.

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)

[*Discovery Reports. Vol. XXXI, pp.* 299–326, *February* 1961)

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THE APPENDAGES OF THE HALOCYPRIDIDAE

By E. J. Iles

(Department of Zoology, The University of Manchester)

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INTRODUCTION

A PROLONGED systematic study of ostracods has impressed me with the remarkably constant pattern of the structure, even to the fine details of setation, of the appendages of the Halocyprididae. In earlier literature (Müller, Claus, Sars, Vavra), brief descriptions of the anatomy of these animals are to be found, but they usually refer only to isolated limbs or to the carapace. More recently Skogsberg (1920, 1946) has given minute details of the structure and setation of appendages in a number of species, but nowhere is there a description of the anatomical and spatial relationship of the various limbs to each other. This is essential to the proper understanding of the functional morphology, the way in which the limbs are used, which, in its turn, is essential as a background to further advances in the study of the taxonomy and thus the evolution of the group. The following paper is an attempt to supply this deficiency.

The family Halocyprididae is included in the Myodocopa, which is characterized as follows: shell generally with an antennal notch; seven pairs of appendages; frontal organ usually present; antenna biramous with well-developed propod, exopod multiarticulate and bearing natatory setae, endopod normally small and often prehensile in the male; mandibular palp pediform; caudal furca with lamellar rami bearing marginal spines. All the members of the Halocyprididae are planktonic and have appendages adapted to this mode of life.

Although numerous species have been studied during the course of my work, one was selected for intensive study, namely *Conchoecia borealis* G. O. Sars var. *antipoda* G. W. Müller, not because it is more typical of the group than any other species, but because material fixed in alcoholic bouin was available in the Discovery collections. This had been very kindly handed to me by Professor H. Graham Cannon. The material was suitable for cutting wax sections which could be used to check certain features of anatomy. Formalin-fixed material also available from the Discovery collections was unsuitable for embedding in wax. It was used, however, for the preparation of thick celloidin sections for study by methods similar to those described by Professor H. Graham Cannon (1933). The greater part of my work on the group, however, has been carried out by the use of fine or microdissection methods. After removing the carapace, antennules and frontal organ, the remaining appendages of the left side of the animal were separated by cutting the arthrodial membranes by which they articulate with the body. By this means, not only could an independent study of the isolated appendages be carried out, but the body of the same animal could be mounted left side uppermost. With sufficient care in dissection, the relationship of the inner faces of the undisturbed appendages of the right side could then be studied. In preserved material the appendages occupy a range of positions which must represent those which they could take up during life. Study of a number of such specimens and the articulation and musculature of their appendages has been of value in interpreting the observations of live animals made by Müller (1894).

Müller (1906), whose figures were quoted by Skogsberg (1920), gave a very wide distribution for

Conchoecia borealis antipoda, between 1° S. and 65° S. in the Atlantic Ocean at depths of 470–1600 m. The Discovery specimens used for study were taken at stations 138, 529, 661, 662 and 671 which ranged from 43° 08′ S. to 57° 36′ S. From the data provided by the samples taken with closing nets the specimens would appear to have been captured at depths greater than 250 m. to below 1000 m. The species would appear to be a deep-water form.

Müller (1906) regarded *Conchoecia borealis* and *C. antipoda* as separate species, but Skogsberg (1920) stated that the differences between them were too small to merit greater rank than that of a variety. Both authors found the females to be larger than the males; the Discovery specimens bear out this difference in size. Skogsberg (p. 718) also found 'that the shoulder-vault had a sharp edge contrary to what is stated by G. W. Müller 1906', both males and females being alike in this character. In the few males examined from the Discovery collections the shoulder-vault was sharp-edged but not quite so far expanded as in the females. Skogsberg described the setation of the appendages in great detail, but some repetition and further discussion has been found necessary in this report.

The intensive study of *C. borealis antipoda* leads on to a comparison with other halocyprids, e.g. *Archiconchoecia*, *Euconchoecia* and *Halocypris* and to a comparison of this group with the Cypridinidae.

ACKNOWLEDGEMENTS

I wish to thank the National Institute of Oceanography, and in particular Dr Mackintosh and Dr Bargmann, for making their valuable collections available to me for study. My thanks are especially due to Professor H. Graham Cannon for his continued encouragement and interest in my work.

THE APPENDAGES, THEIR INTERRELATION AND FUNCTION

Antennules (Figs. 1 and 2)

The antennules are uniramous and exhibit sexual dimorphism. Their shafts articulate antero-dorsally with the body of the animal, close beneath the hinge of the carapace. They are normally directed straight forward.

In the male (Fig. 1 B) each is rigidly bound to the long slender shaft of the frontal organ by a single pair of inner dorsal hooked seta. The three terminal setae are of great length. Of these latter, the principal and one of the secondary setae bear an armature of spines and setules, which lock them together for part of their length. Only the apices diverge. This armature differs in other species and is a specific character of differential value. The setae are directed forward and slightly downward through the anterior gape of the carapace. By flexure of the apical articles of the antennule, they can be folded back and beneath the animal, between the bases of the appendages. Besides the principal and secondary seta there are two so-called 'tube-setae' near the apex of the antennule. These are much shorter than the principal setae, stout, bluntly ending and very thin walled.

In the female (Fig. 1 A) the shafts of the antennules are not locked to the frontal organ. The inner dorsal setae extend forward to just beneath the rostrum. A single apical seta, corresponding to the principal seta of the male antennule, is extended forward and downward, but its length is such that it extends only slightly beyond the margin of the carapace (Fig. 2, $a_1 s$). The secondary setae of the female are similar to the sensory tube-setae of the appendage of both sexes. In both sexes these terminal tube-setae are carried hanging downward within the anterior gape of the carapace.

It would seem that in the halocyprids the function of these appendages is largely sensory, though there is no experimental evidence of this. The thin-walled tube-setae are of a type similar to other 'chemo-sensory' setae found in the Crustacea. They lie directly in the path of the water-current flowing through the carapace, because they hang vertically in its anterior gape. The principal setae,

as already mentioned, show sexual dimorphism and specific variation in their armature, and may have some special secondary sexual function. The fact that in some species, even in the male, their free tips have a structure similar to the sensory tube-setae may mean that they also are sensory.

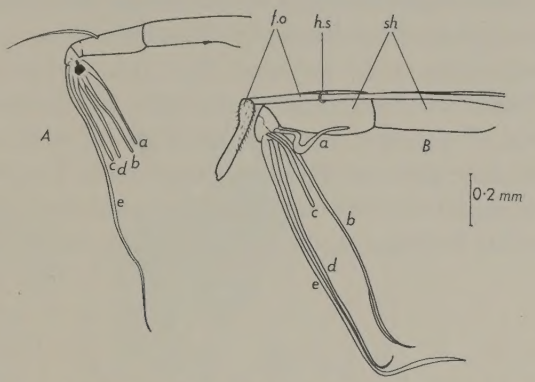

Fig. 1. *Conchoecia borealis antipoda.* Right antennule from inside. A, female; B, male with frontal organ. *f.o.* frontal organ; *h.s.* hooked seta; *sh*, shaft; *a* and *c*, tube setae; *b* and *d*, secondary setae (tube setae in female); *e*, principal seta.

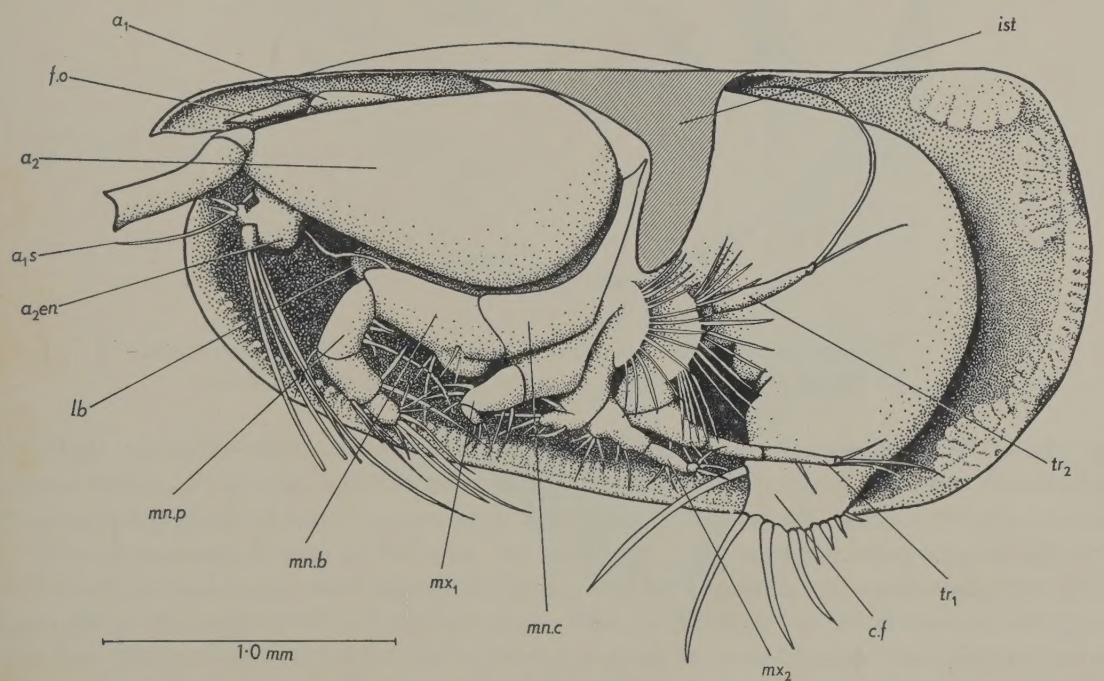

Fig. 2. *C. borealis antipoda.* Female with left valve of carapace removed, antennal exopod omitted. a_1, antennule; a_1s, principal seta of antennule; a_2, antennal shaft; a_2en, antennal endopod; *c.f.* caudal furca; *f.o.* frontal organ; *ist*, isthmus linking body to carapace; *lb*, labrum; *mn.b.* mandibular basis; *mn.c.* mandibular coxa; *mn.p.* mandibular palp; mx_1, maxillule; mx_2, maxilla; tr_1, first trunk limb; tr_2, second trunk limb.

Antennae (Fig. 2, a_2, Fig. 3)

The antennae are biramous with the exopod composed of eight or nine articles and the endopod small with not more than three articles. The endopod shows sexual dimorphism. As in most Myodocopa, each relatively enormous, broadly expanded shaft contains a powerful musculature. Each articulates

antero-laterally with the body just behind the antennules and extends straight forward. The multi-articulate antennal exopod with its long natatory setae is similar in both sexes. It articulates somewhat to the outside of the apex of the shaft, the articulation corresponding exactly in position with the base of the antennal notch of the carapace (Fig. 2). It can be extended through this notch or withdrawn into the carapace and then lies beneath the body of the animal, with its natatory setae embraced by the palps of the mouth-parts and the bases of the first trunk-limbs.

The broad, flattened basal article of the endopod (Fig. 3) articulates with the shaft on its inner surface near the apex. It bears two short setae which differ in structure in different species. The second article bears two setae of moderate, but unequal length, of which at least the apices are thin-walled. Besides these, in the male there are three very short setae, but not more than one of them is present in the female; in the female of *Conchoeia borealis antipoda* they are all absent. The end-article bears three 'tube-setae' similar to those of the antennule. In the male there is a clasping organ

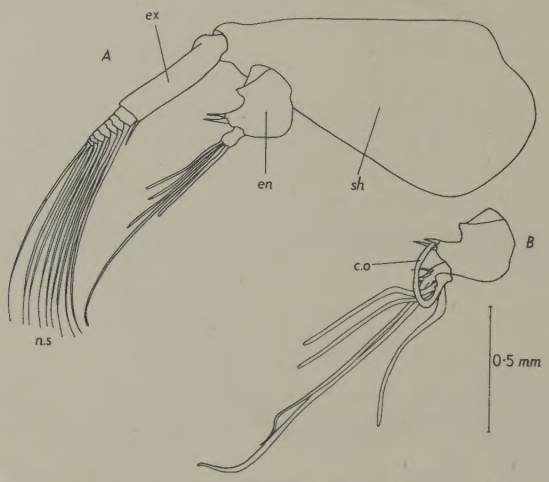

Fig. 3. *C. borealis antipoda*. Right antenna from inside. A, female; B, endopod of male. *c.o*, clasping organ; *en*, endopod; *ex*, exopod; *n.s*, natatory setae; *sh*, shaft.

(Fig. 3 B, *c.o*) which Skogsberg (1920) considered to be a modification of the end-article itself. This is a hook-like structure which differs somewhat in form on the two sides of the animal, and also differs in different species. Normally the longer setae of the ramus extend vertically downwards, just within the anterior gape of the carapace; the ramus can, however, be moved antero-posteriorly.

The main adaptation of the antenna is for swimming. The exopod of the appendage can be extended through the antennal notch and moved freely, even when the valves of the carapace are tightly closed. The form of this notch and hollowing of the carapace below and behind it allow free backward movement of the exopod. The exact match in position of the articulation between the antennal exopod and shaft with the notch leads to the notch serving as a rowlock for the backward stroke of the oar-like exopod and its natatory setae. The articulation is bicondylar, with the one condyle ventral and the other dorsal but slightly displaced outward and forward. The main part of the musculature enclosed in the antennal shaft is the flexor musculature of the exopod. Skogsberg (1920) described the swimming action of the antennae and pointed out that it resulted in a forward propulsive stroke. In fact, the bicondylar articulation leads to the exopod swinging back in an arc with a slight downward movement. This downward movement gives a slight uplift to the front of the body exactly like that produced by our arm action in the breast stroke. Uplift in the water will also be produced by the boat-shape of

the carapace. In *Conchoecia borealis*, as in many other species, development of the shoulders of the carapace into sharp flanges provides hydroplanes which also contribute to uplift of the animal when it is swimming. The main component of the swimming-stroke can thus be concerned with forward propulsion.

As has been pointed out, the antennal endopod shows sexual dimorphism. The tube-setae are probably sensory, and in the male the hooked clasping-organ probably had a copulatory function.

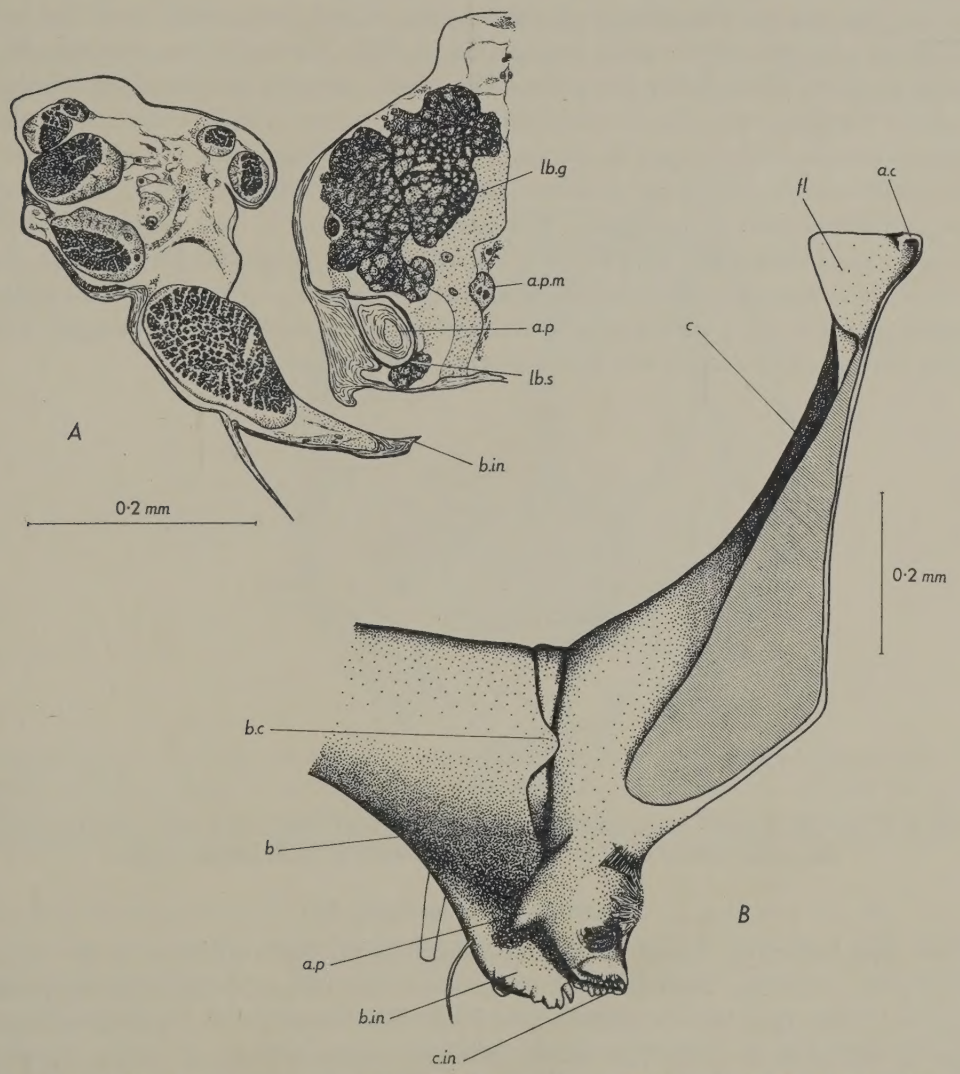

Fig. 4. *C. borealis antipoda.* A, transverse section through labrum and mandibular basis showing distal articular process of coxa in labral socket; B, right mandibular coxa and part of basis from inside. *a.c*, dorsal articular condyle of coxa; *a.p*, distal articular process of condyle; *a.p.m*, antero-posterior labral muscle; *b*, basis; *b.c*, articular surface of basis and coxa; *b.in*, incisor edge of basis; *c*, coxa; *c.in*, incisor edge of coxa; *fl*, anterior dorsal flange of coxa; *lb.g*, posterior labral gland; *lb.s*, wall of labral socket.

Labrum (Figs. 2, 4, 7, 8, 10)

The labrum is well developed and filled with gland-cells. It is usually described as being helmet-shaped. In section, its ventral surface is flattened and its dorsal surface rounded (Fig. 4 A). It arises

ventrally in front of the mouth and projects forward below and between the shafts of the antennae. The vertical posterior surface forms an anterior boundary to the oral atrium (Fig. 8). The atrium is bounded laterally by the mandibles, paragnaths and maxillules, and leads antero-dorsally into the oesophagus, which is directed slightly forward and upward. The posterior wall of the labrum usually bulges back to some extent, between the mandibular coxae. It is, however, provided with antero-posterior muscles (Fig. 4 A, *a.p.m.*), which can draw it forward and so increase the volume of the atrium. It bears a median patch of short, fine, dorsally directed bristles (Fig. 8). Ventrally to the oral atrium, a thin flat surface, with thickened cuticle, extends back horizontally from the labrum like a shelf. This may be termed the labral lamina (Fig. 8, *lb.l*). Laterally, the posterior edge of this lamina takes the form of comb-like structures. The whole posterior surface of the labrum and the labral lamina is supported by sclerites continuous with the ventral sclerite system of the animal.

The labrum contains two systems of glands. The anterior of these consists of a number of large unicellular glands, closely packed and running dorso-ventrally. Their openings are evenly spaced over the ventral and lateral walls of the labrum. The openings can only be seen clearly in heavily stained material (e.g. with chlorazol black), when they appear as small crater-like depressions. The second system is a paired compound gland, the two components of which lie partly within the posterior part of the labrum (Fig. 4 A, *lb.g*), but extend into the body on either side of the oesophagus. These latter glands open through the posterior wall of the labrum into the oral atrium.

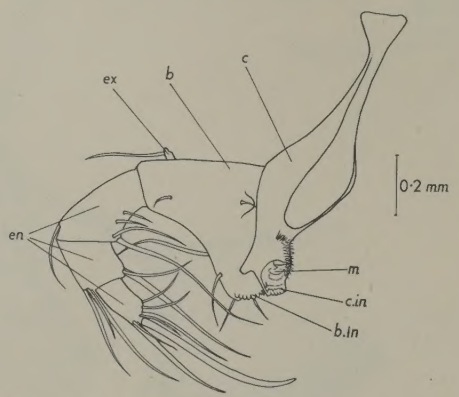

Fig. 5. *C. borealis antipoda.* Right mandible from inside. *b*, basis; *b.in*, incisor edge of basis; *c*, coxa; *c.in*, incisor edge of coxa; *en*, endopod; *ex*, exopod; *m*, molar surface of coxa.

Mandibles (Figs. 4, 5, 6)

Possibly the most interesting feature of the appendages of the Halocyprididae is the structure and articulation of the mandible. Each mandible is biramous, the endopod being large and pediform, the exopod minute. There have been frequent references in the literature to the presence of a gnathobase on its basis as well as on its coxa. This feature is in fact used as a character diagnosis of the whole group.

The *coxa* is elongate (Fig. 4 B, *c*, Fig. 5) and articulates with the side of the body immediately behind the base of the antenna (Fig. 2). The dorsal part is narrow and extends between the base of the antenna and the isthmus which links the carapace with the sides of the body of the animal. The anterior surface of this extension is laterally concave to accommodate the backward swelling of the antennal base. At the apex of the extension there is a cuticular thickening which forms the articular condyle (Fig. 4 B, *a.c*). Just beneath this condyle a rigid triangular flange (Fig. 4 B, *fl*) extends forward. Curving downward and inward below the articulation with the body, the gnathobase

(Fig. 4, *c.in*) extends into the oral atrium. As mentioned above, it forms a lateral boundary to the atrium (Figs. 7 and 8). Anteriorly at this lower end the coxa is produced into a distally directed process (Fig. 4 B, *a.p*), which Skogsberg (1920, p. 570) describes as more or less triangular and 'against which the endite on the following joint rests with an antero-inner edge'. Skogsberg also refers to the term 'Zahnhöcker' adopted by Claus (1891) for this process. In fact the structure is much more rounded than is suggested by these descriptions and is directed (it should be noted) much more nearly parallel to the longitudinal axis of the coxa than is shown in the figures given by Claus (1891, pl. XXII, figs. 6 and 15). The statement that the endite of the following joint rests on it is quite erroneous. No doubt Skogsberg based it upon observations of isolated mandibles. Examination of the appendage *in situ* and in section, shows that the process fits exactly into a thickened socket, which is part of the

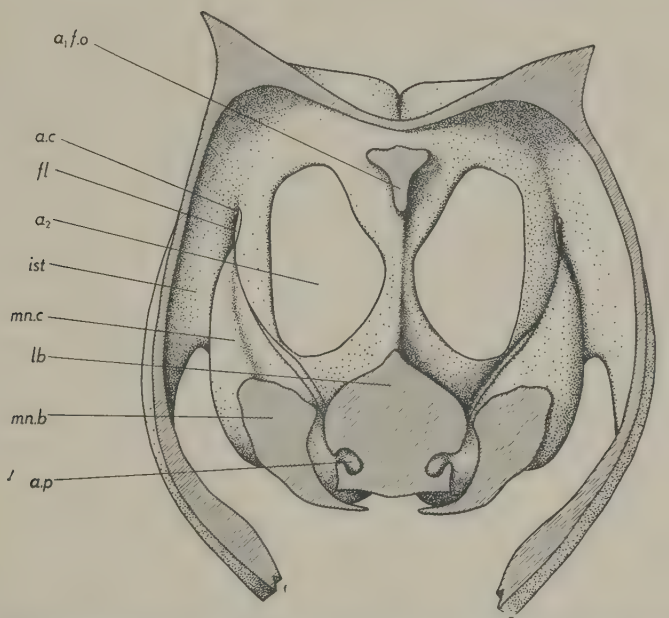

Fig. 6. *C. borealis antipoda.* Diagrammatic anterior view of a thick transverse section through mandibular region. (Antennal shafts omitted to show mandibular coxae.) a_1 *f.o*, base of antennules and frontal organ; a_2, antennal socket; *a.c*, dorsal articular condyle of mandibular coxa; *a.p*, distal articular process of mandibular coxa; *fl*, anterior dorsal flange of mandibular coxa; *ist*, isthmus linking body with carapace; *lb*, labrum; *mn.b*, mandibular basis; *mn.c*, mandibular coxa.

sclerite framework supporting the oral surface of the labrum (Fig. 4 A, *a.p* and *lb.s*, Fig. 8). The projection of this peg into the socket in the labrum is sufficiently deep to make it difficult to remove the appendage during dissection. The mandibular coxa is thus restricted in its movement to rotation about the axis formed by this articular process and the dorsal condyle. This axis, in fact, coincides fairly accurately with the anterior margin of the area of articulation of the coxa with the body (Fig. 4 B). In relation to the body of the animal, the axis of rotation of the coxa extends upwards, sloping slightly outwards and backwards (Figs. 2 and 6).

The mandibular musculature has been figured by Müller (1894, pl. 55). The extrinsic musculature of the coxa is in fact very much more complex than is shown in his figures. Full details of this musculature will not be given here, but it is significant that the arrangement of the muscular elements is such that they will rotate the coxae about the axes which result from their bicondylar suspensions. The anterior dorsal muscles originate near the hinge-line of the carapace and are inserted on the flanges anterior to the dorsal condyles. Since the axes of rotation of the coxae slope markedly out-

wards dorsally, these muscles extend at wide angles to them. Contraction of the muscles will result in outward rotation of the coxae so that their gnathobases separate. The posterior dorsal muscles originate near the anterior dorsals and are inserted on the posterior margins of the coxae. On contraction they will rotate the coxae inwards, bringing the gnathobases together. It is the transverse musculature which is so complex. Elements of it originate on various parts of the anterior hypostomal apodeme, or intermandibular tendons fused to it and on the antenno-labral apodeme. These are inserted on various parts of the coxae. The majority will rotate the coxae inwards, giving a powerful biting action by the gnathobases.

The coxal gnathobase is, as has frequently been pointed out, complex in structure. For the purpose of description it may be considered in four parts. Curving into the oral atrium distally, immediately above the posterior labral shelf, are three parallel incisor edges (Figs. 4, 5, Fig. 8, *c.in*). Although, as Claus (1891) pointed out, the structural pattern is more or less specifically constant, there is in *Conchoecia antipoda*, as in other species, some individual variation. Broadly speaking, the distal ridge, which extends the full width of the gnathobase, is, at least posteriorly, clearly divided into teeth. The middle and proximal ridges are much less regularly toothed, but always bear a long tusk-like posterior tooth. Dorsally to these ridges, the surface is shallowly concave. At the base of this depression there is a ridged pad, the masticatory pad (Fig. 5, Fig. 8, *m*). Skogsberg (1920) describes this as being covered with fine papillae placed close together. Müller (1894) more correctly refers to it as bearing isolated conical spines. These short sharp spines are so closely packed that the surface formed by their tips does in fact give the impression of being papillose. It is only by focusing through their depth in a whole mount, or seeing them in section that a true picture of the structure is obtained. The third region is the posterior margin of the gnathobase. Here there are four stout spines arranged in a dorso-ventral row (Fig. 8, *m.c*). These curve into the oral atrium and radiate slightly along the length of the row. Posterior to these teeth there is a dense group of radiating 'needle spines', each of about the same length as one of the teeth (Fig. 8, *m.f*). The fourth structure is a dorsal group of fine spines, almost continuous in distribution with the posterior group, but directed towards the mouth and projecting slightly into it.

The basis articulates with the coxa so that it extends forward almost at right angles to the latter (Fig. 4 A, Fig. 5). It is clear that its main movement is through a dorso-ventral arc, but rotation of the coxa about its axis will of course move the distal end of the basis laterally inward or outward. On the inner face of the basis, near its distal end, is a fine seta of moderate length, which extends inward across the labrum. At the anterior edge of the gnathobase are two setae, one long and one short, which extend ventrally. On the ventral surface of the gnathobase itself, are two further closely adjacent setae, which also extend ventrally and somewhat posteriorly. Near its distal end the basis bears dorsally a small mamilliform appendix (Fig. 5 *ex*, Fig. 7, *mn.e*), with a long anteriorly directed seta. Müller (1890, 1894) and Skogsberg (1920) have referred to this structure as representing the exopod of the appendage.

Proximally and ventrally a flange of the basis extends inward to form the gnathobase (Figs. 4, 5, *b.in;* Fig. 8). This gnathobase lies ventral and parallel to the incisor edges of the coxal gnathobase. It is separated from the latter by the backwardly projecting labral lamina (Fig. 8). The basal gnathobase consists of a single sharp biting edge formed by a row of six shouldered teeth. It is followed posteriorly by first an isolated spine, then a short, stout, spine-like seta. Ventral to the incisor edge is a single serrated tooth (Fig. 8, *v.t*). On the posterior ventral surface of the gnathobase are a series of short, stout, bristles. The basis and coxa articulate with each other by a fulcrum, which occurs about midway between the distal articular process of the coxa and the upper surface of the joint (Fig. 4 B, *b.c*). It is clear that rotation of the basis about this fulcrum will produce a backward and forward movement of

the gnathobase and this, if the coxa gnathobase remains rigid, will produce a shearing action. Rotation of the coxa will lead to a biting action of the gnathobases of the bases as well as of those of the coxae.

The two apical articles of the three-jointed palp are somewhat flattened transversely. The tip of the palp bears two stout claw-like setae (Fig. 5). These are pectinate on their posterior margins and curve posteriorly towards their tips. One of these claws is equal in length to the palp itself, the other is about two-thirds of this length. Besides these, there is, near by, a more slender seta of about the same length as the shorter claw and also a series of four fine setae of about half this length. A series of setae are present on the anterior margin of the palp. When the palp is folded inwards these extend towards the margin of the carapace. Distally on the middle article is a long stout pectinate seta, which is, however, more flexible than the terminal claws. Its length is such that it extends almost to the apex of the shorter terminal claw. Adjacent to it are two much shorter fine setae. A further short

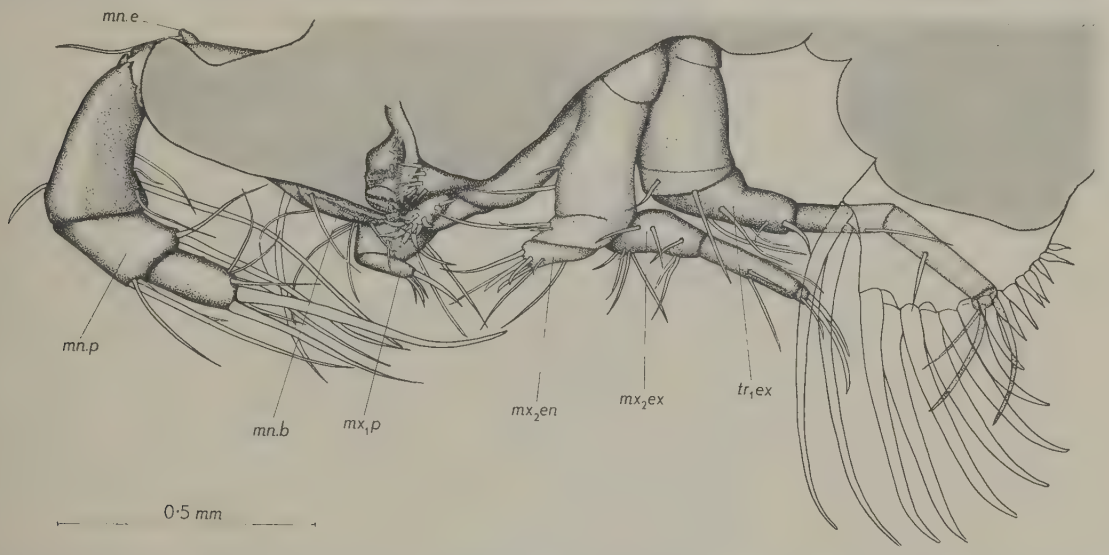

Fig. 7. *C. borealis antipoda*. Mouth and first trunk appendages viewed from mid-line; caudal furca in front of tips of trunk appendages shown in outline; armature of setae omitted. *mn.b*, mandibular basis (gnathobase); *mn.e*, mandibular exopod (mammiliform appendage); *mn.p*, mandibular palp (endopod); $mx_1 p$, palp of maxillule; $mx_2 en$, maxillary endopod; $mx_2 ex$, maxillary exopod; $tr_1 ex$, exopod of first trunk limb.

seta arises near the apex of the proximal article. The posterior margin bears a further series of setae. There are two long pectinate setae of the same form as the long anterior one. The first of these arises near the distal end of the middle article and the other from a similar position on the proximal article. Both reach to near the apex of the shorter terminal claw. The middle article bears a shorter fine seta on its posterior distal margin and the proximal article three similar short fine setae distributed along the distal half of the posterior margin. All the finer setae bear fine secondary setules. The articulation of the proximal article of the palp with the basis is provided with lateral cuticular facets which limit its movement to a dorso-ventral direction. The limits of movement allowed by the articulation would seem to be from a position where the proximal article is directed nearly vertically upward from the basis to one with it directed vertically downward. The second and third articles can be extended straight in line with the proximal article or flexed toward the body. The articulation of the articles in series is such that the palp can be extended upwards and outwards, with the terminal claws near the antennal notch of the carapace, or folded downwards and inwards. Due to a slight diagonal setting of the articulation between the basale and the proximal article of the palp, the downward and inward movement is accompanied by a rotation of the palp about its axis, in such a fashion that the

short anterior marginal setae extend across the labrum towards the middle line (Fig. 10) and the short posterior marginal setae interlace with the ventral setae of the basale (Fig. 7). The length of the palp and that of the basis are such that during the downward arc of movement of the former, first the long posterior marginal setae, secondly the apical claws and lastly the long anterior marginal seta are drawn down the anterior margin of the carapace. At the posterior extreme of this movement, the terminal claws lie between the palps of the maxillulae and the endopodites of the maxillae. The posterior marginal setae lie with their tips pressed against the surface of the labrum. Finally the long anterior marginal seta lies just inside the ventral margin of the carapace, with its apex within range of the claws of the palp of the maxillule.

The outstanding structural features of the mandible are the presence of a gnathobase on the basis as well as on the coxa and the bicondylar articulation of the coxa. Skogsberg (1920, pp. 556–7) has pointed out that the mandible is used for holding food fast and for mastication. With reference to the incisor edge of the basis, he stated that as G. O. Sars (1887) pointed out, 'it seems to have the same function as the cutting part on the mandible of many other Crustacea, while the *pars incisiva* of the coxa serves as a sort of *tuberculum molare*, to break up the food more finely'. He stated that the latter process also serves partly as a 'cutting organ'. The bicondylar suspension of the coxa, which seems to be surprisingly uncommon in the Crustacea, is important in that it will enable an extremely powerful crushing action to be carried out by the gnathobases, while the firm proximal support provided to the palp will facilitate its independent movement. The disadvantage is that the arrangement will strictly limit the size of food-material which can be passed between the coxal gnathobases. Borradaile (1922) has described how in the shore crab (which also has a bicondylar suspension of the mandible) the food is first broken up by other appendages, before passing between the mandibles. In *Conchoecia*, it is difficult to see how, with the possible exception of the maxillules, appendages other than the mandibles could function in this manner. Quite clearly the shearing action of the gnathobases of the mandibular bases must have the function of cutting food into pieces which will pass between the gnathobases of the coxae into the oral atrium. This, as will be shown, is confirmed by the type of food material found in the stomachs of the animals.

The structure of the coxal gnathobase is complex and so also must be its function. It is interesting to note its division into incisor and molar processes in a manner similar to that of the mandibular gnathobase of the Malacostraca. There can be no doubt that the function of the incisor edges of these structures in *Conchoecia* will play an important role in breaking up food material passed between them. It is more difficult to visualize the function of the molar surfaces, with their closely packed spines. These probably would serve to grip and crush food-material, particularly if this were small, soft particles. The row of four teeth on the posterior margin of the molar surface must serve to retain food-material in the oral atrium, which same function in the case of smaller particles would be served by the fringe of fine spines. The fine orally directed spines will clearly aid transport of food-material into the mouth.

In his earlier work, Müller considered that the halocyprids might to a limited extent be bottom-living and use their mandibular palps for walking, as do the cypridinids. It is now clear, however, that they are planktonic during the whole of their life-cycle. This leaves the mandible free for its important role in feeding. The palp with its well-developed apical claws, extending beneath the oral atrium in the flexed position, and its wide arc of antero-posterior movement, is well adapted to grasping food and bringing it within the range of action of the mouth-parts. In dissected appendages it is difficult to see what function the marginal setae of the palp could possess in the whole animal, but when the palps are flexed it is evident that they could aid retention of food beneath the labrum and oral atrium.

Paragnaths (Fig. 8)

In the halocyprids the paragnaths are well developed. They extend ventrally immediately behind and closely investing the hinder margins of the mandibular coxae (Fig. 8, *p.g*). Each paragnath is triangular in shape and almost completely occupies the space between the mandibular coxa and the protopod of the maxillula. The anterior margin, where it borders on the mandibular coxa, is edged with a series of short fine bristles, which extend forward and inward towards the bristles on the margin of the molar surface of the mandible.

Functionally the paragnaths are important because they complete the lateral walls of the oral atrium. The anteriorly directed spinules of their anterior borders aid retention of food material within the atrium.

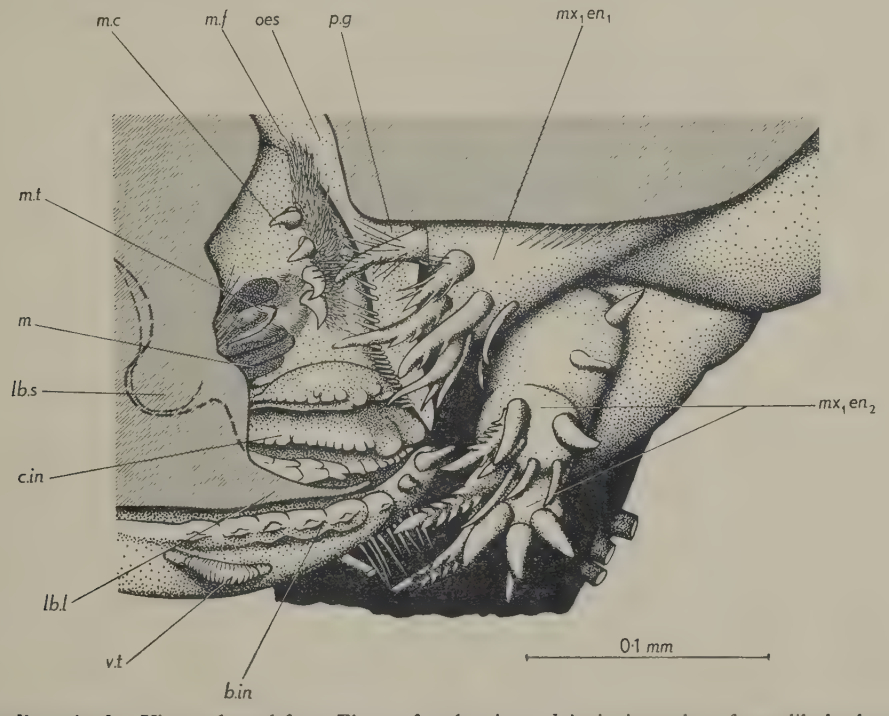

Fig. 8. *C. borealis antipoda.* View enlarged from Fig. 7 of oral atrium. *b.in*, incisor edge of mandibular basis; *c.in*, incisor edge of mandibular coxa; *lb.l*, labral lamina; *lb.s*, labral socket; *m*, molar pads of mandibular coxa; *m.c*, molar claws; *m.f*, bristle fringe of molar surface; *m.t*, molar tooth; mx_1en_1, pre-coxal endite of maxillule; mx_1en_2, coxal endites of maxillule; *oes*, oesophagus; *p.g*, paragnath; *v.t*, ventral tooth of basal gnathobase.

Maxillulae (Figs. 8, 9 & 10)

The maxillulae are uniramous, the endopod forming the palp and the protopod bearing well-developed endites. They arise ventro-laterally, immediately behind the paragnaths and project vertically downwards.

The proximal article of the protopod, generally considered to be the pre-coxa, is very short. The coxa is somewhat longer. There appear to be two endites (Fig. 8, mx_1en_1, mx_1en_2, Fig. 9), the proximal being pre-coxal, the distal arising from the coxa. The latter is, however, deeply bifid. It would seem useful to adopt the view of Müller (1894 *et seq.*) and Skogsberg (1920), who considered this endite to consist of two fused endites, comparable to the two distal endites of the cypridinids. The pre-coxal endite bears a series of stout setae, of which the two nearest the body are brush-setae, the more distal

anterior are pectinate and the remainder spine-setae. The proximal endite arises in the angle between the limb and the body. The ventral body-wall, in preserved material, usually bulges downwards between the proximal endites of the two sides, but is provided with muscles radiating to it from the anterior hypostomal apodeme. It would appear probable that this muscular system is used in conjunction with the labral muscle to enlarge the oral atrium. Depression of the body-wall must be by haemocoelic pressure, and flexure of the body. The middle and distal endites bear a series of powerful, inwardly directed spine-setae. The anterior spine-setae are pectinate with their secondary teeth apically directed. Skogsberg referred to the movable articulation between the articles of the protopod and their well-developed independent musculature. He also pointed out that the endites are not movable in relation to the articles from which they arise. Independent movement of the proximal

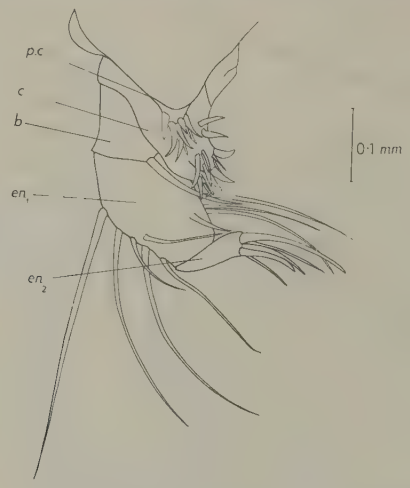

Fig. 9. *C. borealis antipoda.* Right maxillula from inside. *b*, basis; *c*, coxa; en_1, first article of endopod; en_2, second article of endopod; *p.c*, pre-coxa.

articles is great, but may be analyzed into two main components. One movement of each is rotation with respect to the length of the limb, thus swinging its endite through a horizontal arc. The other is a rocking movement which swings the endite through a small vertical arc. Skogsberg pointed out the marked divergence of the direction of the endites with the limb at rest. He did not, however, point out their range of movement or their relation to the other appendages. The proximal (pre-coxal) endites may be more or less directed towards one another across the body when its floor is raised. More usually they are directed forward between the paragnaths toward the incisor edges of the mandibular coxae; then the floor of the body is usually depressed. By an anterior rocking of the limb, their setae are thrust forward and upward between the molar spines of the mandibular coxae, their proximal brush-setae extending almost to the mouth. The coxa can move relative to the pre-coxa but the positions of its endites will also depend upon movements of the latter. The total range of movement of the coxal endites would seem to be from a position where they point straight across the body to one in which they point somewhat forwards and inwards between the mandibular gnathobases. They may be depressed to a position pointing slightly ventrally to the gnathobase of the mandibular basis or elevated so that they point towards the incisor surfaces of the coxa of this limb.

The palp of the maxillula (Fig. 2, Fig. 7 $mx_1 p$, Fig. 9) is generally accepted to be the endopod, but the basipod, which is very short and bears no endite is, as Hansen (1925) pointed out, partly fused with the first article of the endopod. The second article of the palp (first endopod article) is the longest of

the whole appendage. It is broad, being flattened laterally in relation to the animal. On its anterior border it bears a series of four long setae, which extend forward to the region of the outer setae of the basis of the mandible. On the posterior margin there are three long setae which extend ventrally and backwards outside the maxillary endites. The anterior edge and inner face bear three further setae, which extend medially beneath the endites, together with a single seta arising from the inner face of the basis. The terminal article is cylindrical, tapering only slightly towards its apex. In *Conchoecia antipoda* its length is only slightly greater than the width of the previous article and it is normally directed backwards at right angles to the axis of the palp. At its apex it bears a group of five setae. Two of these are stout claws, of which one is about two-thirds the length of the other. Two other setae are more slender, but claw-like, and of about the same length as the shorter main claw. The fifth seta is very slender and about the same length as the longest claw. All of these curve forwards. Müller (1894) stated that the endopod is so bent inwards that it lies nearly parallel to the endites of the stem. It is true that the palp may take up this position, but it may also slope outwards to some extent. Besides this, some antero-posterior movement can take place. The end-article seems only capable of movement through a dorso-ventral arc, relative to the preceding article. The extent of this movement is from a position in line with the rest of the limb to one pointing posteriorly almost at right angles to it. Rotation of the protopod about its axis results in movement of the apical article of the palp through a horizontal arc, so that its total field of action is fairly large. It can be extended backwards with its claws interlacing with those of the maxilla, or extended forwards with them lying over or between the gnathobases of the mandibular basis. It does not, however, seem that the claws can be extended into the oral atrium, or folded inwards sufficiently to reach the endites of the protopod of the limb.

It has been pointed out above, that the maxillulary palps have anteriorly curved apical claws and their movement must be mainly through a horizontal arc. In fact it seems probable that their main function must be to pass food material forward on to the gnathobases of the mandibular bases. The maxillulary endites are well developed, but their armature is very much less powerful than that found in the cypridinids where they are used for mastication of the food (Graham Cannon, 1933). It would seem that in halocyprids they have little masticatory function. The direction in which their few spines and setae point and their range of movement would indicate that the distal endites probably serve to grip food in the mid-line and to transfer it from the gnathobases of the mandibular bases to the region of the incisor edges of the mandibular coxae in the oral atrium. Similarly it seems likely that the proximal endites push food forward on to the molar surfaces of the mandibular coxae and aid transport of food into the mouth.

Maxillae (Figs. 7, 10 & 11)

The maxillae are biramous with one ramus jointed and pediform, the other unjointed. The protopod bears a well-developed epipod.

There has in the past been some variance of opinion regarding which pair of appendages the fifth pair of limbs of many ostracods represent. Graham Cannon (1925, 1926) has shown quite clearly that, on the basis of the segmental excretory organs, in *Cypridopsis vidua* (=*Pionocypris vidua*), they are the maxillae. There is no reason to doubt that they represent the same pair of appendages in the Halocyprididae. Besides this, however, there are almost as many opinions regarding the homologies of the parts of the limb as there have been workers on the group. This is too extensive a topic to consider here in detail. On the basis of the musculature and segmentation of the appendage, it would appear that Skogsberg's view (1920) is reasonable. This view is: that the shaft extending ventrally from the body of the animal (Figs. 7, 11) is the protopod; the inwardly directed distal 'endite' with

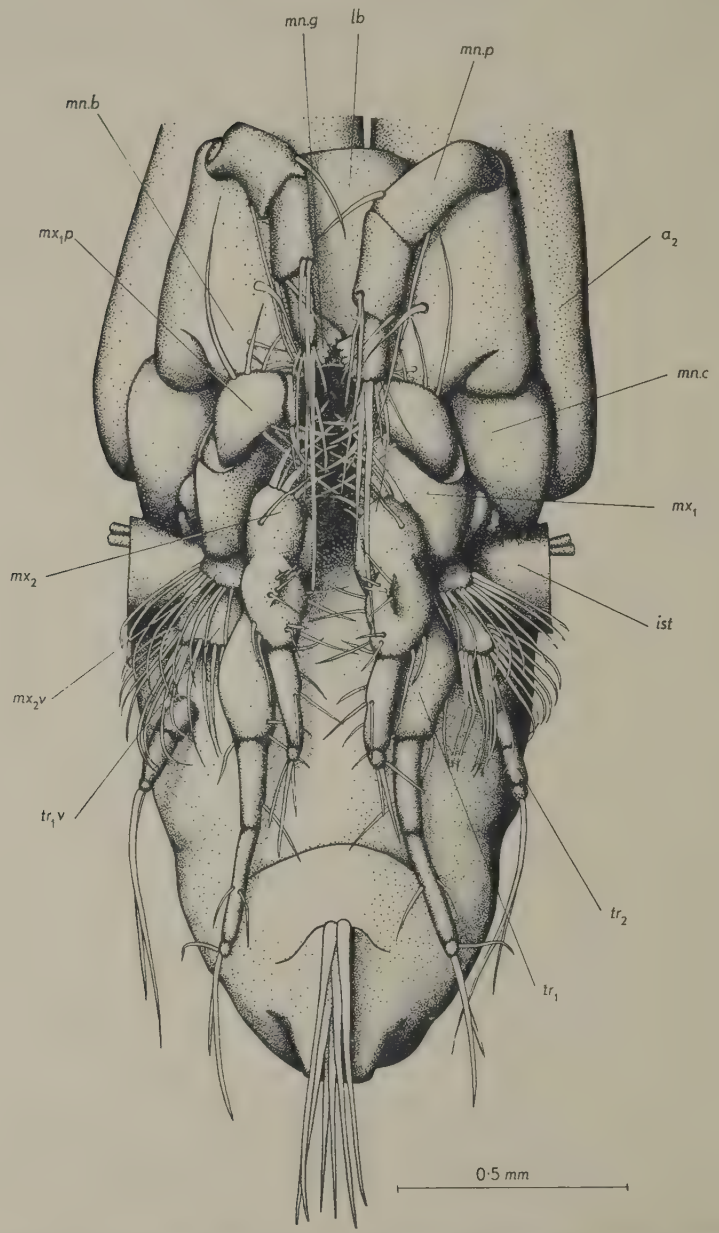

Fig. 10. *C. borealis antipoda*. Ventral view of body (only part of antennae included). a_2, antennal shaft; *ist*, isthmus linking body to carapace; *lb*, labrum; *mn.b*, mandibular basis; *mn.c*, mandibular coxa; *mn.g*, mandibular basal gnathobase; *mn.p*, mandibular palp; mx_1, maxillula; mx_1p, palp of maxillula; mx_2, maxilla; mx_2v, vibratory plate of maxilla; tr_1, first trunk limb; tr_1v, vibratory plate of first trunk limb; tr_2, second trunk limb.

independent musculature (Fig. 7 mx_2en, Fig. 11, *en*) is the endopod; and the long posteriorly directed pediform portion of the limb (Fig. 7 mx_2ex, Fig. 11, *ex*) is the exopod. The vibratory plate would then be an epipod. In general impression the limb is pediform. The protopod normally extends directly ventrally beneath the body from a ventro-lateral attachment, immediately in front of the isthmus,

which links the body of the animal with its carapace (Fig. 2, mx_2). In this position the vertical flattened epipod, in the form of a vibratory plate, extends outwards towards the carapace. Plumose setae, arranged in three groups, extend from the margin of this epipod. At the apex of the protopod is the large anteriorly directed endite-like structure, which, as already mentioned, is probably the endopod of the appendage. This bears at its apex a group of three pectinate claw-setae, which curve inwards and slightly backwards (Fig. 10). Dorsally and externally to them are three moderately long, anteriorly directed brush-setae. The setae of the endopod may be directed towards the apical claws of the maxillularly palp, but forward movement of the shaft of the maxilla brings them into the region of the distal endites of the maxillule. A degree of ventral extension of the endopod is also possible. Proximal to the endopod, there are on the shaft of the maxilla two groups of setae, borne on slight prominences, which probably represent endites. There are three setae in thedistal group, a long outer brush-seta, a median brush-seta of about half its length and an extremely short inner seta. The more

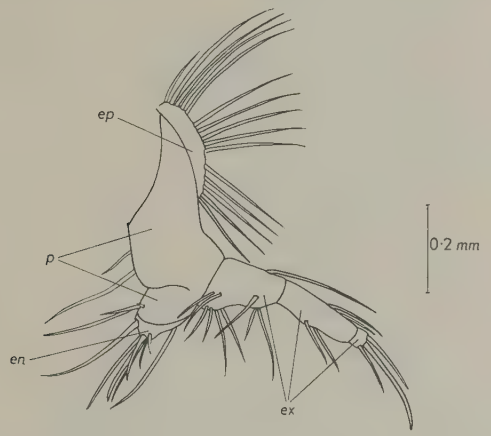

Fig. 11. *C. borealis antipoda*. Right maxilla from inside. *en*, endopod; *ep*, epipod; *ex*, exopod; *p*, protopod.

proximal group consists of a brush-seta of about the same length as the longest in the distal group and a much shorter seta. The setae in these two groups are directed towards the distal endites of the maxillule, though their position varies with movement of the shaft and they can be directed more dorsally towards the proximal maxillulary endites.

The exopod (Figs. 7, 10 and 11) is divided into three articles. The first two of these are long, the terminal very short. The articulation of this ramus is slightly to the outside of the distal extremity of the protopod and at rest extends back parallel to the body of the animal. At the apex of the exopod there are two long claw-setae which curve downwards, and a much more slender one. From the lower edge arise a series of setae extending downwards. These setae are in series with a long brush-seta extending downwards from the ventral surface of the endopod. Of them, there are four in a group arising from a prominence at about a third of the length of the proximal article from its base. A further pair arise near its apex. The second article bears a similar single seta about the middle of its length. A second series of setae arise from the median face of the exopod and extend inwards across the mid-line. There are on the first article two of these near to the proximal group of ventral setae and a third near the distal pair. The second article bears a single medially directed seta near its ventrally directed seta. Somewhat dorsally from the outer face arise a third series of setae, which extend backwards, upwards and slightly outwards. Two of these are near the apex of the proximal article and a third arises at about two-thirds of the length of the second article.

Besides the antero-posterior movement of the shaft of the maxilla, the exopod is capable of similar movement. In preserved material it usually lies parallel to the margin of the shell, with its terminal claws directed straight back. It may, however, be flexed ventrally to produce a curvature of the limb, while the terminal article may be flexed so far that the claws are directed vertically downwards at right angles to the remainder of the limb. Professor A. C. Hardy has pointed out to me, in a personal communication, that the live animal quite normally extends the whole limb vertically downwards. Such a movement will draw the ventral setae and terminal claws forward along the ventral posterior margin of the carapace and bring the whole maxilla within reach of the inward arc of movement of the mandibular claws.

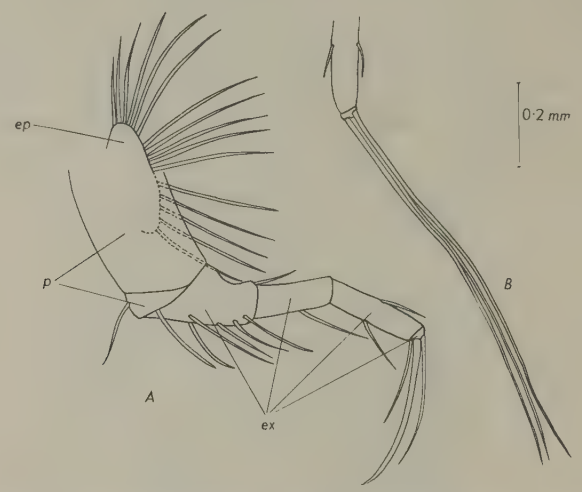

Fig. 12. *C. borealis antipoda*. A, female right first trunk limb from inside; B, apex of the same appendage in male. *ep*, epipod; *ex*, exopod; *p*, protopod.

With its wide range of antero-posterior movement and ventrally curved terminal claws, the elongate exopod of the maxillae may play some part in collection of food. The short endopods, with posteriorly curving claws, probably play a main role in food transport in conjunction with the maxillulary palps. The endites, as described above, are very poorly developed. Their long slender brush-setae may assist in forward transport of fine food-material, but can be of little use for manipulation of larger material. Marginal setae of the exopod may aid retention of food-material.

The epipod of this appendage, in conjunction with that of the first trunk-limb, undoubtedly creates a respiratory water-current through the carapace in a manner similar to that in *Cypridopsis* (= *Pionocypris vidua*) and in *Cypridina* described by Graham Cannon (1926, 1931). Müller (1894) had in fact observed this current in *Conchoecia* experimentally with the aid of carmine particles. He also described how the epipods beat continuously and independently of other movements of the limbs.

First trunk-limbs

The first trunk-limbs are uniramous, jointed and pediform. The protopod bears a well-developed epipod. They show sexual dimorphism. Though very similar in general appearance to the maxillae, as pointed out by Skogsberg (1920), their endopods are even less well developed. The protopod of each arises immediately behind that of the maxilla so that it extends ventrally below the posterior extreme of the isthmus linking the body of the animal with the carapace. It bears an epipod similar to that of the maxilla. As might be expected from its position in relation to the protopod of the

maxilla, it bears no endites and no setae. The part of the limb which Skogsberg considered as the endopod bears a single long brush-seta extending forward towards the mid-line of the animal (Figs. 7 and 12). The exopod of the appendage (Figs. 7, 10 and 12) has four articles, the proximal being the longest, the distal, as in the case of the maxilla, being the shortest. In the female, there are two distal claws and a seta, similar to those of the maxilla, but in the male there are three extremely long natatory setae, which can curve upwards as far as the hinge-line of the carapace. Further setae on the exopod may be described as similar to those of the maxilla. Projecting ventrally there is a single apical seta on the inner face of the protopod in series with two further setae on the first article and one on the third article. Projecting towards the mid-line from the inner face are three setae on the first article, one on the second and one on the third. There is only one seta extending outwards from the limb, on the first article of the exopod. In addition, however, there are further setae (not represented) on the maxilla—a dorsal distal seta on the first article of the exopod and a dorsal medial seta on the third article.

Movement of the limb would seem to resolve into an antero-posterior movement of the protopod and a dorso-ventral extension and flexure of the exopod. The ventral flexure of the limb may not be as great as that of the maxilla but the dorsal extension is greater.

The epipods of these appendages beat in conjunction with those of the maxillae. It is possible that the limbs themselves could take part in collection of food, but the enormously elongate apical setae in the male are strongly suggestive of some function of locomotion in this sex.

Second trunk-limbs (Figs. 2 & 13)

The second trunk-limb (Fig. 2, tr_2, Fig. 13) is very short with three articles. It arises at the side of the body just behind the first trunk-limb. At rest it is directed dorsally and posteriorly. The only setae arising from this appendage are two apical setae, one of which is very long, extending to the posterior dorsal margin of the carapace and the second of which is only half the length. Müller (1894) described the movement of this appendage in some detail. Apparently, as its structure suggests, it is extremely mobile; it can be flexed or rotated freely.

The immediate function which comes to mind in the case of these limbs, with their position high on the side of the body of the animal and extreme mobility, is that of cleaning. Müller, however, pointed out that these limbs cannot reach the epipods of the maxillules and maxillae, the most obvious structures to require cleaning. Furthermore he described how these structures are self-cleaning. Müller was, in fact, not able to observe the second trunk-limb performing any definite function. Some doubt must thus remain about this.

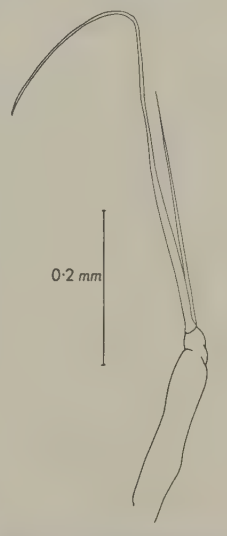

Fig. 13. *C. borealis antipoda*. Left second trunk limb from outside.

Furca (Figs. 2 & 7)

The furca of the Myodocopa is so well known as to need little more than brief mention. Each furcal plate bears eight claws, an anterior group of four large ones and a posterior of four smaller ones. All eight claws radiate outwards from the furca, the most anterior one, which arises from the anterior border of the furcal plate, pointing markedly anteriorly. The more posterior claws point slightly backwards. All the claws are bipectinate on their posterior margins. Antero-posterior flexure of the trunk of the animal and hence antero-posterior movement of the caudal furca, can be considerable. Thus the trunk may be stretched out straight posteriorly to extend the caudal furca through the

posterior gape of the carapace, or it may be flexed forward to bring the furcal claws between the bases of the appendages. In this latter position, the anterior claws extend between the endites of the maxillules, with their apices almost in the oral atrium. There can be no doubt that these claws have a cleaning function as is commonly the case in ostracods.

Penis

The structure of the penis of the halocyprids has been described by Skogsberg, but though his and earlier descriptions make it difficult to understand the three-dimensional structure of the organ, this is not in itself relevant to the present topic. It is, however, worthy of note that this extremely large organ is unilateral and set well to the side of the animal. In this position, though it extends downwards to the ventral margin of the carapace, or even beyond, it does not impede the movement of the limbs and leaves a clear path for the flexure of the trunk and anterior extension of the caudal furca.

FEEDING-MECHANISM

Type of food

Müller (1894, 1927) stated that the stomachs of halocyprids contained the remains of copepods. He further stated that these have been trapped on the sticky shell, drawn in by the mandibular palps and conveyed with the sticky secretion of the shell-glands into the mouth and stomach. Elofson (1941) also found copepod remains in the stomachs of certain species of *Conchoecia* and I too have found such copepod remains in the stomachs of numerous species. I have even seen a specimen of *C. bispinosa*, which had a large part of the crushed but only slightly dismembered exoskeleton of a small copepod in its stomach; usually, however, the only identifiable remains are limbs, but it has not been previously noted that these are usually derived from animals of a size equal to or greater than that of the ostracod. It is difficult to understand how large prey could be trapped in a sticky secretion of the carapace, unless this secretion was much more copious than would be indicated by the size and number of the glands. In fact, the stout spines and claws present on the mandibles and maxillules, together with the powerful gnathobases of the former, give the impression of a voracious predator.

I have noticed that, whether or not there are any copepod remains in the stomach of a halocyprid, there is usually a mass of fine material. This confirms Müller's observations (1894); but in addition the material sometimes contains diatom remains, a fact not stated by Müller. The type of food contained in the stomach bears little relation to the size of the animal. Thus, some stomachs of the large *C. valdiviae* have been found to contain nothing but fine detritus while, on the other hand, those of the comparatively small *C. echinata* have had limbs and other remains of copepods obviously from animals larger than the ostracod. Diatoms and other fine detritus could have been derived from the copepods which had been eaten; frequently, however, as has been stated, such material may be present without any copepod-remains. Furthermore, the appendages, particularly the proximal endite of the maxillule, have, in addition to spines, an armature of slender setae and brush-setae, which is reminiscent of a particulate feeder (cf. *Cypridina antarctica* according to Graham Cannon, 1933).

Feeding on fine material

Whether diatoms or detritus are deliberately collected by *Conchoecia* as food or are swallowed accidentally is difficult to decide. There is no trace of any filter-feeding-structure in these animals, but there are two ways in which such material could be collected. Müller's description of the observations upon which he based his conclusions regarding the feeding of halocyprids provides evidence regarding one of these.

Müller described (1894, p. 109) how carmine particles, suspended in water in which *Conchoecia*

was swimming, became trapped in the sticky secretion of the marginal glands of the carapace. He observed this to be drawn in by the mandibular palps and formed into a mass by the mouth-parts. He pointed out that this process took place whether anything was trapped in the secretion or not. Elsewhere (p. 127) he stated that he was not able to observe directly that it was swallowed, but found that the stomach contents were similar in nature to this material. It is perfectly clear, from the structure of the mandibular palps, that they could draw in the secretion of the marginal glands from the front half of the carapace, as observed by Müller. The apical claws are suited to such function (Fig. 2), while the posterior marginal setae and possibly also the anterior marginal setae could contribute to the process. Müller (1894) held the view, repeated by Calman (1909), that the greater development of the anterior marginal glands of the carapace may be associated with this process. It is not, however, universally true that these glands are better developed than the others. In fact, if anything, *Conchoecia antipoda* has them less well developed. It would be possible, however, for the secretion from the more posterior parts of the ventral margin to be drawn forwards by the anterior curving claws of the maxillary exopod (Fig. 2). The possibility of the limb moving in this fashion has already been considered (page 316). The secretion could thus be brought within range of the movement of the claws of the mandibular palps and added to any food collected directly by them. The only appendages which can reach the posterior margin of the carapace, which is also provided with numerous glands, are the second trunk-limbs. Their fine setae are poorly adapted to movement of such material, while their range of movement could hardly bring it within reach of other appendages. Thus although food-material may be trapped by secretion from the glands of the carapace, these cannot be entirely subservient to this function.

The structure of the appendages shows that Müller's statement, that food-laden secretion dragged in by the mandibular palps is passed into the oral atrium by the palps of the maxillule, probably does not cover the whole process. It is improbable that the movement of these structures would be sufficient to pass material directly into the oral atrium. When the mandibles are folded under the body, their claws extend into the field of movement of the maxillary endopods (Fig. 7) which with their backwardly curved claws could easily withdraw material from the mandibular claws. The maxillulary palps, with their forwardly curved claws could then draw food-material forward from the maxillary endopods to bring it below the labrum in the region of the mandibular gnathobases.

The other possible method of collection of fine material is quite different. I have frequently noted that preserved material may have a mass of detritus held beneath the labrum by the open cage of setae formed by the infolded mandibular palps. This could of course have been passed forward by the maxillulary palps, and could also be contained in the secretion from the marginal glands of the carapace, which has been swept in by the posterior marginal setae of the mandibular palps. There is, however, another possible explanation for the presence of detritus in this region. The beat of the epipods of the maxillules and maxillae creates a water-current through the carapace, and will carry detritus with it. Müller (1894) has, indeed, described how detritus is carried in this manner in the live animal. A large part of the water-current must flow between the mandibular palps and over the surface of the labrum in just that region where the numerous openings of the anterior labral glands are situated. This resembles the food-collection mechanism described by Graham Cannon (1933) in *Cypridina*. There is no information available regarding the nature of the secretion of the labral glands in *Conchoecia* but, if it is comparable with that of other crustacea, it will be a sticky secretion which will entangle any detritus swept in with the water-current, as in the case of *Cypridina*. The secretion together with the detritus would then be held in place by the marginal setae of the mandibular palps and be available as a source of food-material. Whether detritus is collected in this manner beneath the labrum of *Conchoecia* as food-material can only be determined experimentally.

But by whatever means fine material is collected, it seems that it will be massed beneath the labrum, and that transport to the oral atrium must follow. It has been pointed out already that the downward arc of movement of the mandibular basis brings the incisor edge backwards and upwards into line with the distal endites of the maxillule. By this means the posterior spines and setae of the basal gnathobases, together with the gripping action of the incisor edges, could transport food-material into the path of forward-movement of these endites. By their shearing action, the basal gnathobases may at the same time cut up any larger material trapped in the secretion. During the upward arc of movement of the mandibular bases, the lateral combs of the labral lamina would retain material in the oral atrium.

Though the transversely directed spines of the distal maxillulary endites could play some part in trituration of food, it seems likely that this would mainly be with large material. It is possible that the peculiar structure of the molar pads on the mandibular coxae is an adaptation for trituration of fine material. Certainly such material, trapped in sticky secretion, would be retained between them by the fringing spinules on the posterior margin of the coxal gnathobase and on the anterior borders of the paragnaths. Forward thrusting of the proximal endites of the maxillules, with their brush-setae and pectinate spines (Fig. 7) together with that of the few long brush-setae of the maxillary endites, would all the time tend to move material forward and upward towards the mouth. Here the orally directed spinules of the coxal gnathobases of the mandibles, together with the spinules on the oral wall of the labrum, would finally bring food into the mouth. Peristaltic action of the oesophagus would then take over.

During the whole feeding-process, the marginal setae of the appendages must aid retention of material in positions where it can be manipulated by the appropriate appendages.

Feeding on large material

Despite his observations of live specimens, Müller quite clearly did not observe a *Conchoecia* feeding on a copepod. He found the copepod remains in the stomachs of specimens and related this to his observation of the way in which the animal collected the secretion of the marginal carapace glands with carmine particles trapped in it. He did not take into account the size of the prey. There is, then, no direct evidence that the secretion of the glands of the carapace is involved in capture of copepods. A powerful swimmer such as *Conchoecia* should easily capture a copepod, with the aid of its clawed mandibular palps. Whether the sticky secretion of the carapace glands, or perhaps the labrum, aid such capture by immobilizing the prey can be determined only by observation.

Copepod remains which are found in the stomachs of halocyprids are of such size that they would pass betweeen the bases of the trunk-limbs and mouth-parts. They usually show some evidence of crushing. From a specimen with an almost intact copepod in its stomach, it seems likely that captured prey swallowed without being broken up into smaller portions is crushed by the mouth-parts just sufficiently to enable digestion to take place. The initial grasping of such prey by the mandibular palps may possibly be aided by the maxillary exopods, the claws of which are apposed to those of the mandibular palp. It has been pointed out already (page 309) that, during inward flexure, the mandibular palps point slightly inward and rotate appreciably about their axes. Such movement would draw any prey inward and upward and press it firmly against the ventral surface of the labrum. The maxillulary palps could then help to grip the prey. A ventral movement of the apices of the mandibular bases will bring the shearing action of their gnathobases into play, but small prey would be moved back to pass between the bases of the appendages. In this position, manipulation of the food could be aided by the maxillulary palps and the maxillary endopods. Once the anterior end of the prey has

been moved back clear of the labrum, the maxillulary endites could, with their strong spines, grip it and probably to some extent crush it. A forward and upward thrusting of the endites would progressively move the prey through the oral atrium into the mouth. The angle at which the oesophagus leaves the oral atrium is of importance, in that there is no hindrance to direct passage of food into it. During transport of prey into the oral atrium, it would be subjected to further crushing by the coxal gnathobases of the mandibles, while the four posterior molar spines would aid transport by gripping the prey during the recovery movement of the maxillules.

It has been noted that the portions of larger copepods contained in the stomachs of *Conchoecia* are of such a size that they would just pass between the bases of the limbs and into the oral atrium, but the large specimens from which they are derived will not be able to pass. Each must be held below the level of the labrum mainly by the mandibular palps. The incisor edges of the mandibular bases could then shear portions, particularly limbs, from the prey. The slight rotation of the coxa, necessary to carry out this process, and the slight downward movement of the apices of the bases, would not prevent the palps from continuing to hold the prey in position. The secretion of the anterior labral glands could then entangle portions broken free and simplify their retention by the appendages. Further transport of these fragments probably resembles that of small whole prey.

THE APPENDAGES IN OTHER HALOCYPRIDIDAE

In order to add to the overall picture of the Halocyprididae it is of interest to compare the appendages of *Conchoecia* with those of other genera. A detailed comparison must, however, be postponed until more species of these other genera have been studied. Some characteristic features, however, may be considered. In *Euconchoecia* and *Archiconchoecia*, particularly, the setation of the antennule and the secondary sexual characters of the antennal endopod of the male differ from those of *Conchoecia* but, apart from differences of the mandibular gnathobases and the enormously elongated terminal setae of the male first trunk-limb of *Euconchoecia*, the remaining appendages are closely similar in structure and interrelation in all genera. Of particular note is the fact that the mandibular coxa has an articulation with the labrum similar to that described on page 307 in *Conchoecia*. Not only does this show a functional similarity in the mandible, but it also provides a new taxonomic character common to the genera.

Among the halocyprid genera, differences may be seen in the structure of the molar surface of the mandibular coxa. Skogsberg (1920, p. 740) questioned the homologies of the masticatory pad and the oval cavity on the coxa of *Euconchoecia*. In *Conchoecia*, the molar pad is in fact situated in a slight depression, though this is less marked than the depression in the coxa of *Euconchoecia*. The main differences between this latter genus and *Conchoecia* would appear to be as follows. In *Euchonchoecia* the small sharp conical bristles of the central and proximal parts of the molar pad are absent. On the posterior and oral surface of the molar surface of the coxa, there are up to twelve or thirteen molar claws instead of only four as in *Conchoecia*. The marginal bristles are much less dense and the orally directed group seems to be absent. These latter are functionally replaced by the more proximal marginal claws. Skogsberg further pointed out that the claws can be folded inwards into the oval depression. The functional significance of this is unknown, but may be some adaptation to the transport of food in the oral atrium. The structure of the molar surface differs less in *Archiconchoecia*. The molar spine (Müller's spine 'D') is absent, and the molar claws and bristles are less well developed. The structure of the molar surface in the genus *Halocypris* has been discussed by Skogsberg (1920). In *H. globosa* it is very similar to that of *Conchoecia*. *Halocypris brevirostris* differs particularly in the absence of marginal molar claws. The condition in other species of the genus has not been described.

Skogsberg (1920, p. 584) considered, like Müller, that Claus was not justified in placing *H. globosa* in the separate genus *Halocypria*, since the differences were of 'so slight a nature'. He had not then studied *H. globosa* and when later (1946) he redescribed this species he revised his views somewhat. He then considered that in many ways the species was intermediate between *H. brevirostris* and *Conchoecia*. A definite decision on this question must be deferred until other species of the genus have been redescribed, but in view of the small variation in the structure of the coxal gnathobase in *Conchoecia* and the differences in other genera, it seems likely that Claus was justified in his opinion. The two species should probably be placed in at least separate sub-genera, if not separate genera.

Müller (1906) described the interesting species *Thaumatocypris echinata*. In many ways this resembles the halocyprid genera; in particular the mandible possesses a gnathobase on the basis as well as on the coxa. The maxilla and first trunk-limb are similar to those of the halocyprids and bear similar vibratory plates. Though its distal article differs from, the maxillule somewhat resembles, that of *Conchoecia*; there are, however, many differences, the most remarkable of which would appear to be the absence of an antennal notch. This would seem to be related to the fact that though the antennal shaft and exopod are similar to those of the halocyprids, the endopod also is well developed and has a natatory function. In addition the antennule is distinctly segmented and is possibly natatory (Skogsberg, 1920, p. 119). In relation to these differences Skogsberg discussed the stabilizing effect of the spines on the carapace. It is also noteworthy that the caudal furca differs from that of the halocyprids. It would be interesting to know if the mandible has a similar articulation to that of the other halocyprids. Müller's figures (1906, pl. VI) indicate that there are many differences in the incisor edges of the mandible, while the molar surface must be of quite different structure. In addition the terminal setae of the mandibular palp are elongate and not claw-like. The figures and description give no reference to any process on the coxa, which could represent the articular process of other halocyprids. If such an articulation is absent, it would add further weight to the differences between the *Thaumatocypris* and the other halocyprids. The impression is that Müller was justified in placing his species in a sub-family separate from that including the other Halocyprididae.

COMPARISON OF HALOCYPRIDIDAE AND CYPRIDINIDAE

Skogsberg (1920) compared the morphological details of the appendages of the Halocyprididae with those of the Cypridinidae, but did not compare the whole animals from a functional viewpoint. Graham Cannon (1931, 1933) has made such a comparison between the Cypridinidae and the Podocopa. A similar comparison with the Halocyprididae is of interest.

An immediately obvious difference between *Conchoecia* and a cypridinid is the form of the carapace and the antennal notch (Fig. 14). In the former group, the carapace is usually elongate with a straight hinge-line and is very light and delicate; in the latter it is generally rounded with a curved hinge-line and is heavily calcified. The antennal notch of *Conchoecia* extends back very nearly parallel to the hinge-line with a well-developed rostrum above. Behind the notch, the surface of the carapace is hollowed to allow free backward swing of the antennal exopod. In the Cypridinidae the antennal notch is narrower and usually slopes upward towards the hinge-line; there is no prominent rostrum. Associated with differences in the carapace there is a difference in posture of the animal. In a typical cypridinid the main axis of the body slopes anteriorly upward much more markedly than it does in *Conchoecia*. The ventral apodemes, which are similar in the two groups, indicate an upward curvature of this axis much further forward in *Conchoecia* than in *Cypridina*. The nervous system, also, extends further to the posterior in *Conchoecia* (cf. Claus, 1891, pl. I, fig. 11 and Graham Cannon, 1931, fig. 10B). The antennal shaft adds to the appearance of anterior uptilting in *Cypridina*.

In many members of this genus it is as broad as it is long and its longitudinal axis slopes upward. In *Conchoecia* it is elongate and extends forward. The orientation of the body of *Conchoecia* is similar to that of the Podocopa and it is possible that this is more primitive. It is, however, suggested that the orientation of the body and arrangement of the antenna and antennal notch is partly adapted to differences in the mode of swimming in the two groups. As has been mentioned when considering

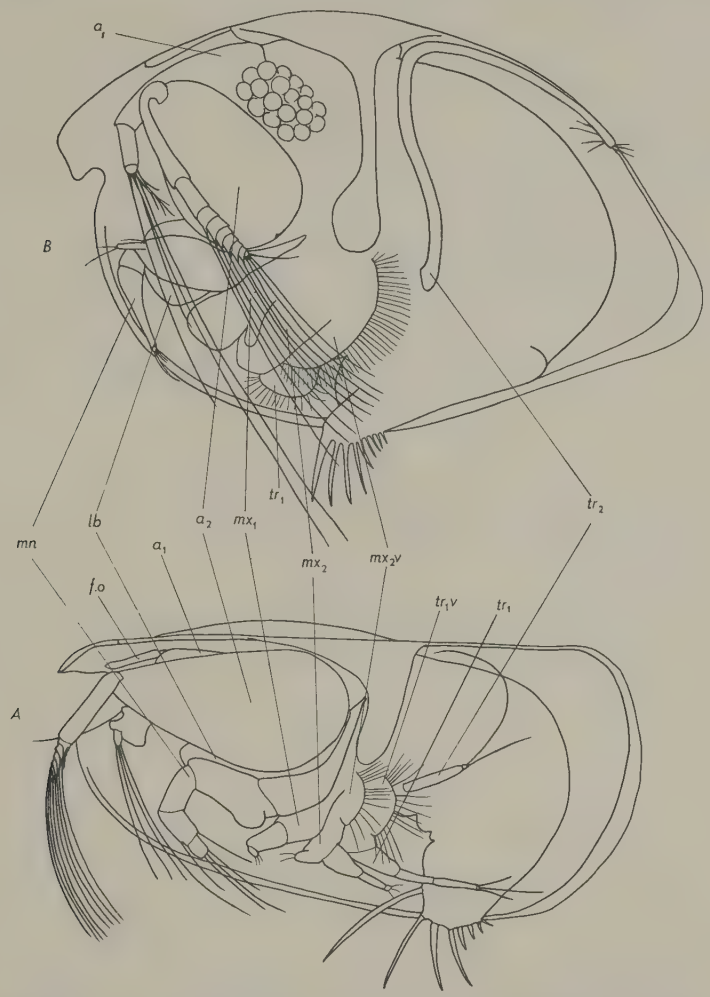

Fig. 14. Diagrams comparing A, *C. borealis antipoda*, and B, *Cypridina* (*Macrocypridina*) *castanea*. a_1, antennule; a_2, antenna; *f.o*, frontal organ; *lb*, labrum; *mn*, mandible; mx_1, maxillule; mx_2, maxilla; mx_2v, vibratory plate of maxilla; tr_1, first trunk limb; tr_1v, vibratory plate of first trunk limb; tr_2, second trunk limb.

the function of the antenna, the swimming action in *Conchoecia* is a forward propulsive stroke with only a small downward component, associated with the light, boat-shaped carapace. In the Cypridinidae, though there is a forward propulsive stroke (as mentioned by Skogsberg (1920)) the greater downward component is associated with the heavy, often rounded carapace. Even in those Cypridinidae such as *Cyclindroleberis* which have an elongate carapace, the body and antennal shaft have a marked upward slope anteriorly. It is interesting that in the genus *Halocypris* where the carapace is heavy and rounded rather like that of a typical cypridinid, the orientation of the body and antennal shaft also is more like that of a cypridinid; and the antennal notch is also more shallow.

The other interesting comparison is the adaptation of the appendages for feeding. Graham Cannon

1931, 1933) has pointed out that in the Cypridinidae there has been a backward shift in adaptation of the limbs for this purpose. Here, instead of the mandibles, the maxillules and maxillae are the main biting-mouth-parts. This is accompanied by a more posterior position of the mouth relative to the appendages. Thus the mouth lies posteriorly to the mandibular coxae, the oral atrium being bounded laterally by the maxillulae; the paragnaths are not developed. In *Conchoecia*, however, like the Podocopa, the mandibles are the main biting-mouth-parts, with the maxillulae playing only a small part in the process and the maxillae not adapted at all for biting the food. In this genus the mouth lies between the mandibular coxae, which also laterally bound the oral atrium, and the paragnaths are well developed. The difference in adaptation of the appendages for feeding is correlated with adaptation for walking. Thus in bottom-living cypridinids the mandibular palp is used for walking and the mandible is no longer used for biting the food. The gnathobase is reduced and adapted merely to assist transport of food into the mouth. The same pattern is retained in planktonic members of the group, such as *Gigantocypris* (see Graham Cannon, 1940), or *Cypridina* (*Macrocypridina*) *castanea* (see Graham Cannon, 1933) which is illustrated for comparison with *Conchoecia* in my Fig. 14. In the Podocopa, on the other hand, it is the antennal endopod which is used for walking and this leaves the mandible free for biting the food. *Conchoecia* does not walk at all and the mandible is free for biting the food. The palp, though well developed, differs in structure from that of the Cypridinidae and is used for capture of food.

SUMMARY

The functional interrelation of the appendages and their setae in *Conchoecia borealis antipoda* is described. Apart from differences in secondary sexual characters, there is little difference in other members of the genus *Conchoecia*.

A new feature of the articulation of the mandible with the body has been found in the Halocypridae. A distally directed condyle on the distal apex of the coxa articulates in a skeletal socket on the oral surface of the labrum. This with the usual dorsal condyle restricts movement of the coxa to rocking about a vertical axis.

The anterior dorsal extrinsic muscle of the mandibular coxa is inserted on a flange which extends forward from the region of the dorsal condyle. This muscle thus serves to rotate the coxae outward and separate the mandibular gnathobases.

It has been confirmed that members of the genus *Conchoecia* are mainly predators on copepods. The method of capture and mastication of such food is discussed. The gnathobase of the basis of the mandible is probably concerned with reducing such food to a size that can be swallowed.

It seems probable that *Conchoecia* species can also feed on fine material. This may be collected by the secretion of the marginal glands of the carapace or by labral gland secretion.

The appendages of *Archiconchoecia*, *Euconchoecia* and *Halocypris* are in general similar in structure and arrangement to those of *Conchoecia*. Their mandibles have the same type of articulation. There are, however, differences in the gnathobases of the mandibular coxae, which must result in functional differences needing investigation.

The differences in the gnathobases of the mandibular coxae of *Halocypris globosa* and *H. brevirostris* are probably of sufficient significance to warrant inclusion of these species in separate genera, as suggested by Claus.

A redescription of *Thaumatocypris echinata* Müller is necessary, in order to clarify its systematic position.

Conchoecia is compared with *Cypridina*. The functional pattern of the mandibles and more posterior limbs of the former, as well as the position of the mouth, do not show the backward shift present in Cypridinidae.

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